Ecology, 67(1), 1986, pp. 258–260

THE CORRELATION BETWEEN RANGE SIZE AND LOCAL ABUNDANCE OF SOME NORTH AMERICAN BIRDS[1]

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Bock and Ricklefs (1983) compared range size and average within-range abundance for 65 taxa of seed-eating songbirds wintering in the continental United States and southern Canada, using data taken from Audubon Society Christmas bird counts (CBCs) for the years 1962–1971. Range size was computed as the number (out of 51) of occupied 5° blocks of latitude and longitude, while abundance was quantified as the log of the mean number of individuals counted per party-hour of count effort for all CBCs in occupied blocks. They reported significant positive correlations between these measures of range size and abundance for all 65 species and for the 22 species >90% restricted in winter to the study area. Splitting the 22 endemics or near-endemics into two groups based on range size, they also found a greater mean within-range abundance in the 11 more widespread taxa than in the 11 more narrowly distributed forms.

The range size–abundance correlations found by Bock and Ricklefs (1983) involve a positive bias, which results from their method of calculating average within-range abundances. Smaller correlations may have been obtained if data were analyzed with a finer scale of geographic resolution. They included all CBCs (each conducted over a 24 km diameter circle) in a given occupied 5° block, even if the species occurred in only a small portion of that block. R. C. Lacy (*personal observation*) found, through a series of computer simulations, that species with small ranges (≤10 of the 51 blocks) would appear less abundant by this method, simply because a larger proportion of their occupied blocks would be on the margin of the species range and only partially occupied. That is, the proportion of zero CBCs within the 5° blocks presumably would be greater among data used to calculate within-range abundances for the species with small ranges than it would for species with large ranges.

This effect can be eliminated by comparing range size with a measure of within-range abundance using only nonzero CBCs for each species. In the present study we used CBC data to compute such fine-scale measures of average within-range abundance for the same species analyzed in the earlier study. We then (1) compared these for the narrowly distributed vs. widely distributed endemic forms, and (2) correlated range size and within-range abundance (as measured using nonzero counts only) for both the endemics and for all 65 species.

Methods

The nature, strengths, and limitations of CBC data, and methods for handling them, have been reviewed elsewhere (Bock and Root 1981). In order to obtain an abundance data set independent of that used in the earlier study, we sampled individual CBCs that occurred in the winter of 1982–1983 and (for rare species) up to three previous winters. From these, we computed mean abundance per party-hour for nonzero counts only, for each of the 65 species (see Bock and Lepthien 1976 for a species list). Three of these taxa recently have been submerged (American Ornithologists' Union 1983), but we have retained them as distinct forms to be consistent with Bock and Ricklefs' data set. (Lumping these forms somewhat increased the correlations found.)

We randomly sampled two 1982–1983 counts published for each province and state, and then one additional count per state and province as many times as was necessary to obtain a sample of at least 25 nonzero counts per species. Certain rare species did not occur on 25 counts in 1982–1983, in which cases counts from up to three preceding years were included

TABLE 1. Spearman rank correlations between range size (number of occupied 5° latitude–longitude blocks) and mean abundance (birds per party-hour count effort) on Christmas bird counts for seed-eating songbirds wintering in the United States and southern Canada.

	Correlations	
	All 65 species	22 species†
Range size vs. mean abundance in occupied 5° blocks (old method)	0.56***	0.64***
Range size vs. mean abundance only in occupied 24 km diameter circles (new method)	0.41***	0.40*
Mean abundance in occupied blocks vs. mean abundance in occupied circles	0.87***	0.89***

* $P < .05$, *** $P < .001$.
† 22 taxa >90% restricted to the study area in winter (endemics).

until that sample size was achieved. Omitting zero counts will overestimate mean abundances, perhaps especially of the rare species, because the species might not have been detected in some count circles where they were very uncommon. Range sizes were calculated as the number of occupied blocks, using CBC data from the previous study for the period 1962–1971. By this method, an error (overestimation) in range size estimation will be proportionately greater for narrowly distributed species than for widely distributed species, because species with small ranges would only partially occupy a larger proportion of occupied blocks. Overall, the methods used in the present study somewhat overestimated mean abundance of rare species and range size of narrowly distributed species. These errors in the estimation of range size and abundance would not have created an artificial association between range size and abundance and, in fact, would have made our analysis of trends conservative.

Range size and abundance data sets were examined for normality using Kolmogorov-Smirnov one-sample tests. The distribution of log-transformed abundance measurements was not significantly different from normal, but the distribution of range sizes was. Therefore, Spearman rank correlations were used to examine the association between range size and abundance, while t tests were used to compare log-transformed average within-range abundances of narrowly vs. widely distributed species.

Results and Discussion

Correlations between range size and average within-range abundance on nonzero CBCs were significantly positive, both for the 22 endemics and for all 65 species; however, correlations were weaker than those found by Bock and Ricklefs using nonzero 5° block abundances (Table 1). Mean $\log_{10}$ within-count abundance of the 11 widely distributed endemics was significantly greater than that of the 11 endemics with smaller ranges (Table 2). In fact, block abundances of the widespread species were greater than nonzero CBC abundances of the narrowly distributed endemics (Table 2, $.05 < P < .10$), despite the fact that the first figure includes many zero count CBCs. Overall, the two abundance measures were highly correlated for both groups of species (Table 1).

In many kinds of organisms, widely distributed species have been found to have the highest local densities (Brown 1983). However, it is important to consider the geographic scale at which density is calculated. If large areas outside of the ranges of narrow endemics are included in the estimations of abundances, then the local abundances of these species will be underestimated. In the present case, range size was more strongly correlated with abundance as measured at the scale of 5° blocks of latitude–longitude than at the scale of 24 km diameter CBC circles, although correlations were significantly positive at both levels. Since most CBC circles include a variety of habitats, it remains to be determined if the wide-ranging species actually outnumber their locally distributed relatives within individual habitats where both occur.

TABLE 2. Average abundances in Christmas Bird Count data ($\log_{10}$ birds per 1000 party-hours count effort) for 11 narrowly distributed and 11 widely distributed seed-eating songbirds wintering in the United States and southern Canada.

	$\log_{10}$ abundance			
	$\bar{X}$	SD	t	P
All counts in occupied 5° latitude–longitude blocks (old method)*				
Locally distributed species	1.765	0.791	4.28	<.01
Widely distributed species	2.947	0.459		
			1.76	<.10
Nonzero counts only (new method)				
Locally distributed species	2.437	0.847	2.79	<.02
Widely distributed species	3.254	0.475		

* Data on counts in occupied blocks modified from Bock and Ricklefs (1983).

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